

CLIMATE CHANGE AND THE DEVELOPMENT OF  
COASTAL PLAIN DISJUNCTIONS IN THE CENTRAL  
GREAT LAKES REGION

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**ABSTRACT.** Paleoecological studies at Portage Marsh in northwestern Indiana provide a Holocene record of local populations of four species disjunct from the Gulf and Atlantic Coastal Plains: *Rhynchospora macrostachya*, *R. scirpoides*, *Fuirena pumila*, and *Eleocharis equisetoides*. The populations were established at Portage Marsh when water levels dropped owing to regional climatic drying during the mid-Holocene. They persisted until the late Holocene; only *R. macrostachya* still occurs in the marsh. Populations of these and other Coastal Plain disjuncts probably were established in the southern Lake Michigan region following mid-Holocene drying and formation of extensive shallow wetlands by coastal processes. Seed sources for these populations may have been in the eastern Great Lakes region. We propose that development of Coastal Plain disjuncts in the central Great Lakes region consisted of a sequential series of westward range-shifts in response to climate-induced habitat changes, rather than a single late-glacial migration along a corridor of suitable habitat.

**Key Words:** biogeography, paleoecology, disjunct populations, climate change, Great Lakes

Scattered populations of plant species with Gulf and Atlantic Coastal Plain affinities occur in the central Great Lakes region (Peattie 1922; Reznicek 1994). These species typically have extensive distributions on the Coastal Plain, ranging from southeastern Texas to southern New Jersey and occasionally southern New England, and are absent or rare through most of the North American interior. In a recent review of the geography, ecology, and conservation biology of the disjunct populations, Reznicek (1994) noted that most of the disjuncts are emergent Cyperaceae and Poaceae that occur in shallow wetlands and lakeshores with fluctuating water levels. Although concentrations of the disjunct species occur in several areas in the central Great Lakes region, the most extensive and diverse is the southern Lake Michigan region of northwestern Indiana and southwestern Michigan (Reznicek 1994). Unfortunately, most Indiana populations have been

extirpated owing to extensive wetland destruction during the past century (Wilhelm 1990).

The Coastal Plain disjunctions have long intrigued ecologists and biogeographers (Peattie 1922, 1930; McLaughlin 1932; Cain 1944; Keddy 1981, 1983; Keddy and Reznicek 1982, 1986). Reznicek (1994) reviewed hypotheses proposed to explain the disjunctions, which range from long-distance dispersal to late-glacial migration along a corridor of suitable habitat extending along the ancestral Great Lakes and their outlets. These and other explanations are difficult to test empirically, however.

The difficulty of testing biogeographic explanations based on past events is widely recognized (Wood 1972; Brown and Gibson 1983; Stuckey 1993). Paleoecological studies are a powerful tool for testing disjunction hypotheses, because pollen and plant macrofossils provide direct records of past occurrences and distributions of species (Whitehead 1972). For example, plant macrofossil studies of late-glacial sediments in New England and the eastern Great Lakes region have been used to test explanations for disjunct ranges of high-arctic and cordilleran species in southeastern Canada (Miller and Thompson 1979; Miller 1987, 1989, 1993).

We have completed a paleoecological study of Portage Marsh in northwestern Indiana that provides a long-term record of local populations of four Coastal Plain disjuncts: *Eleocharis equisetoides* (Elliott) Torr., *Fuirena pumila* (Torr.) Sprengel, *Rhynchospora macrostachya* Torr., and *Rhynchospora scirpoides* (Vahl) Griseb. (Singer et al. 1996). That record, combined with recent advances in understanding of the Holocene climatic history of the Great Lakes region (Baker et al. 1992, 1996; R.S. Webb et al. 1993; Singer et al. 1996), provides a framework for evaluating the origin of the disjunction. We describe here our paleoecological results, summarize the postglacial geological, paleoecological, and paleoclimatic history of the Great Lakes region, and discuss potential mechanisms responsible for the Coastal Plain disjunctions.

#### MATERIALS AND METHODS

Portage Marsh, a shallow, 18 hectare marsh in the towns of Portage and Garyton in northwestern Indiana (Figure 1), is among the few remaining undrained or unfilled marshes in northwestern



Figure 1. Location of Portage Marsh site in eastern North America.

Indiana outside Indiana Dunes National Lakeshore. The site is on shore sediments deposited between 12,200 and 13,000  $^{14}\text{C}$  years Before Present (yr B.P.) during the Glenwood II phase of ancestral Lake Michigan (Chrzastowski and Thompson 1992). The marsh has been disturbed by human activity during the past century. The landscape surrounding the marsh is urban; before the 1950s the landscape was predominantly agricultural. Marsh vegetation

is dominated today by *Carex lasiocarpa* Ehrh. and *Calamagrostis canadensis* (Michx.) P. Beauv., with scattered patches of *Typha latifolia* L., *Dulichium arundinaceum* (L.) Britton, and *Cephalanthus occidentalis* L. Open water patches (ca. 0.6 m deep in summer 1994) are occupied by *Proserpinaca palustris* L., *Potamogeton gramineus* L., and *Utricularia vulgaris* L. A complete list of plants observed in the marsh is provided in Singer et al. (1996). Plant nomenclature follows Gleason and Cronquist (1991). Of the Coastal Plain species, only *Rhynchospora macrostachya* has been observed in the modern flora and seed bank of the marsh.

We analyzed pollen and plant macrofossils from two sediment cores (Singer et al. 1996). Core 1 was obtained using a land-based vibracorer (7.6 cm diameter) and included a complete sequence of Holocene and late-glacial sediments. Core 2, which included only the top meter of sediment, was collected using a modified Livingstone piston-corer (10.2 cm diameter). Both cores were taken approximately 75 meters from the northern edge of the basin, where sediments are deepest. Sediment age estimates were based on radiocarbon dating of both cores.

Sediment samples (50 cm<sup>3</sup> each) were dispersed, sieved (710 and 355  $\mu$ m mesh), and scanned at 6.5 $\times$  magnification using a stereomicroscope for macrofossil analysis. All well-preserved macrofossils (including fruits, seeds, conifer needles, microsporangia, and oöspores) were identified by comparison with herbarium-documented reference specimens. All specimens were assumed to be constituents of the modern flora of the southern Lake Michigan region (Peattie 1930; Deam 1940; Voss 1972, 1985; Swink and Wilhelm 1979). Notes on morphological criteria used in macrofossil identification are provided in an Appendix in Singer et al. (1996).

Sediment samples for pollen analysis were prepared using standard dispersion and digestion procedures, suspended in silicone oil, and scanned at 400 $\times$  (Singer et al. 1996). Pollen percentages for terrestrial taxa were calculated based on a sum of all arboreal, shrub, and upland herb types. Cyperaceae pollen was not included in that sum. Pollen percentages for wetland and aquatic plants, including Cyperaceae, were calculated from a sum of all terrestrial, wetland, and aquatic types.

## RESULTS

Pollen and plant macrofossils from sediment cores provide a record of regional upland and local aquatic/wetland vegetation for the past 11,000 years (Singer et al. 1996). The pollen percentages for tree taxa, *Ambrosia*, and Poaceae (Figure 2) primarily represent vegetation on the surrounding regional uplands. Some Poaceae and most Cyperaceae pollen probably derives from wetland vegetation in the basin. Plant macrofossils (Figures 3 and 4) record local vegetation within the Portage Marsh basin.

The pollen record during the late-glacial interval (>10,000 yr B.P.) indicates regional vegetation consisting of open forest dominated by *Picea* spp. (Figure 2), together with *Abies*, *Larix*, *Populus*, and *Pinus banksiana* Lambert (Singer et al. 1996; Jackson et al. 1986; Webb et al. 1983). During this period, the basin was occupied by an open, hard water lake. Plant macrofossils are rare in the marly sediments of this period.

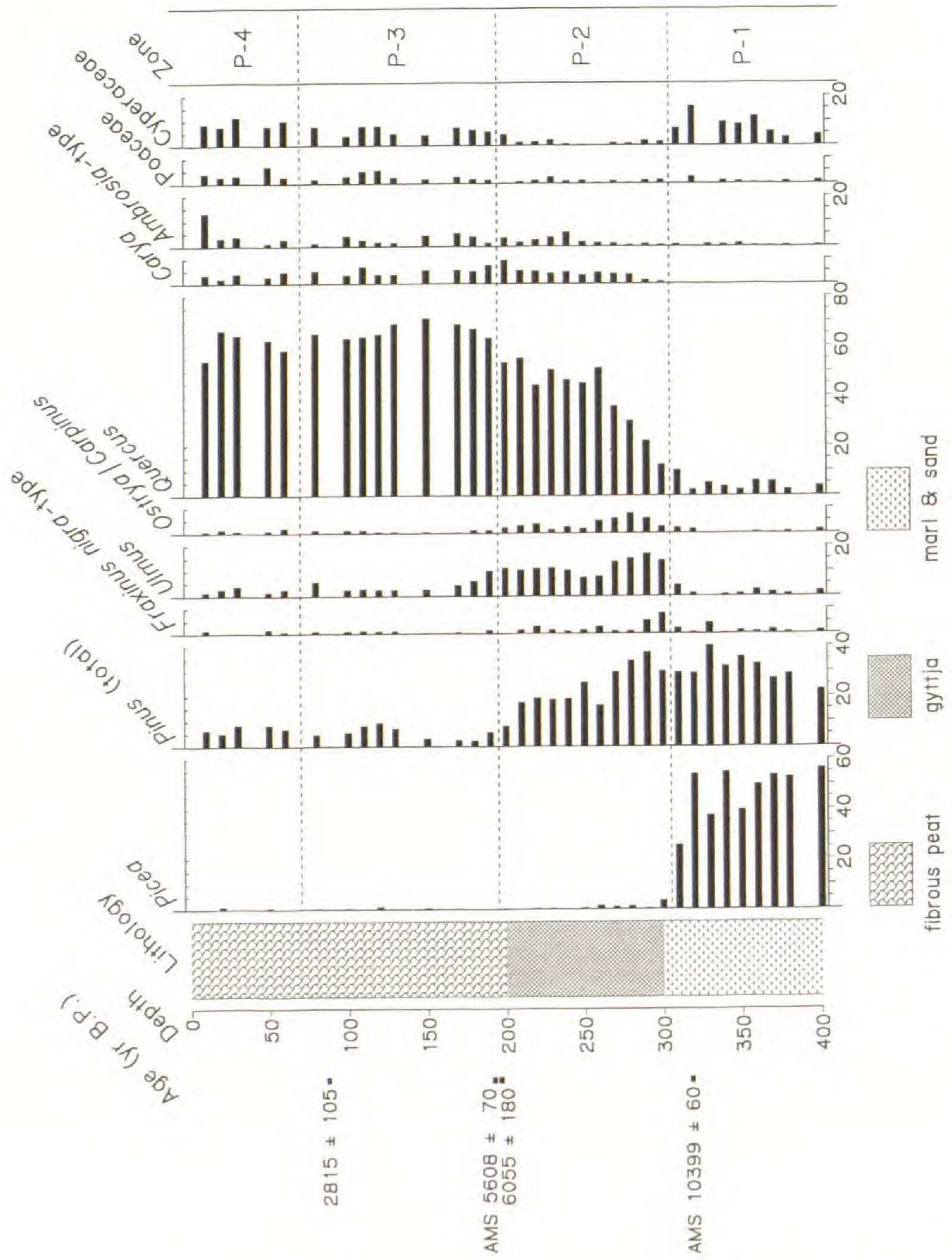
Between 10,000 and 5700 yr B.P., regional vegetation consisted of mixed, mesic forests of *Ulmus*, *Ostrya/Carpinus*, *Pinus strobus* L., *Fraxinus nigra* Marshall, *Quercus*, and *Carya* (Figure 2). The basin was occupied by a lake containing submersed plants [*Najas flexilis* (Willd.) Rostk. & Schmidt, *Chara* sp.; Figure 3]. Emergent plants were scarce in the basin, and sediments consisted of fine-textured algal lake mud (gyttja).

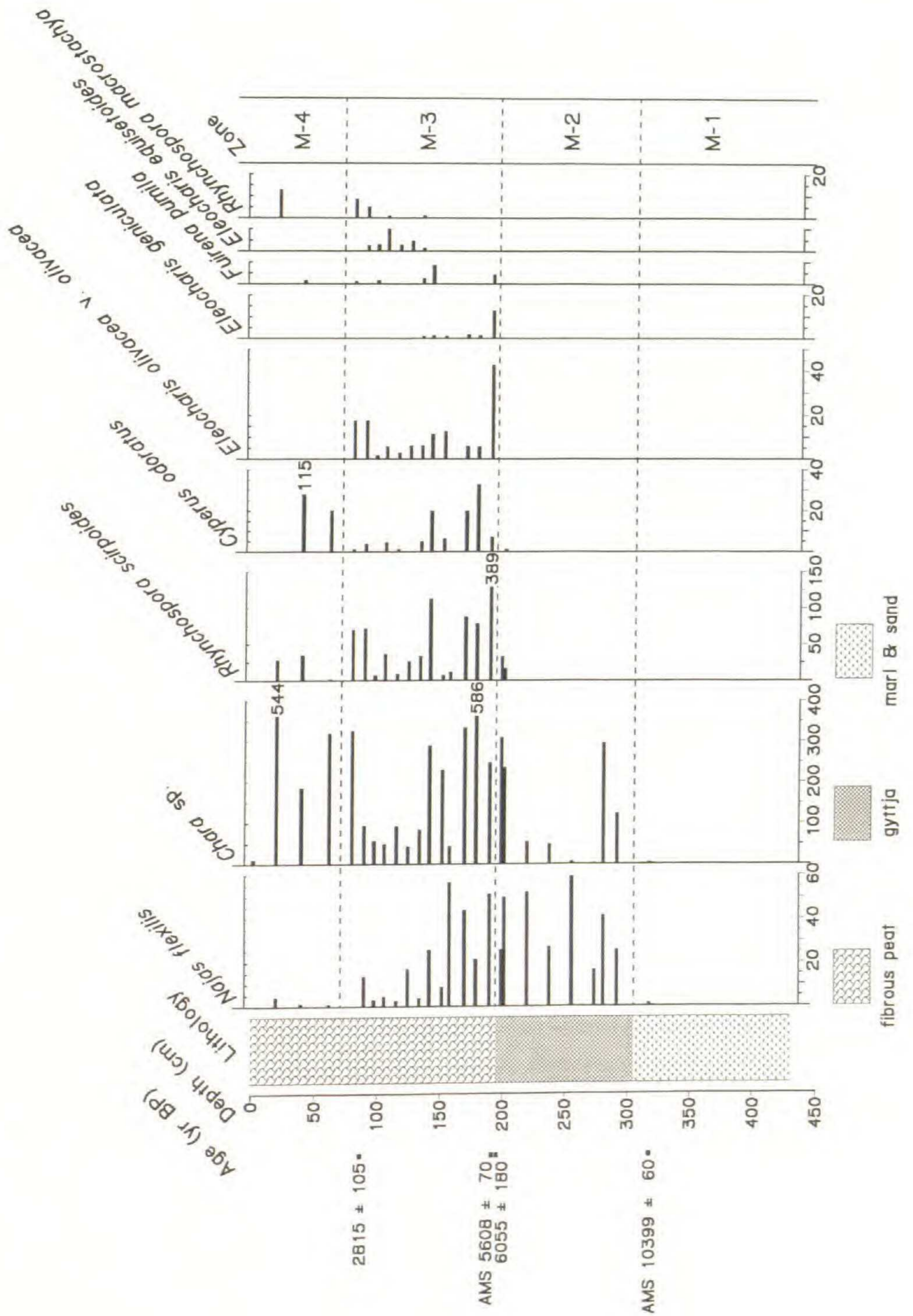
Between 6000 and 5500 yr B.P., the mesic forests of the region were replaced by *Quercus* savanna (Figure 2). At the same time, water levels in the Portage Marsh basin dropped rapidly, leading to development of a shallow, peat-forming marsh with a diverse assemblage of emergent plants (Figure 3). Many of the emergents are annuals or perennials characteristic of exposed shorelines and mudflats during temporary drawdown events. The occurrence of submersed (*Najas flexilis*, *Chara*, *Potamogeton* spp.) and floating-leaved plants (*Brasenia*) together with the drawdown emergents in the assemblages indicates a regime of interannual water level fluctuations.

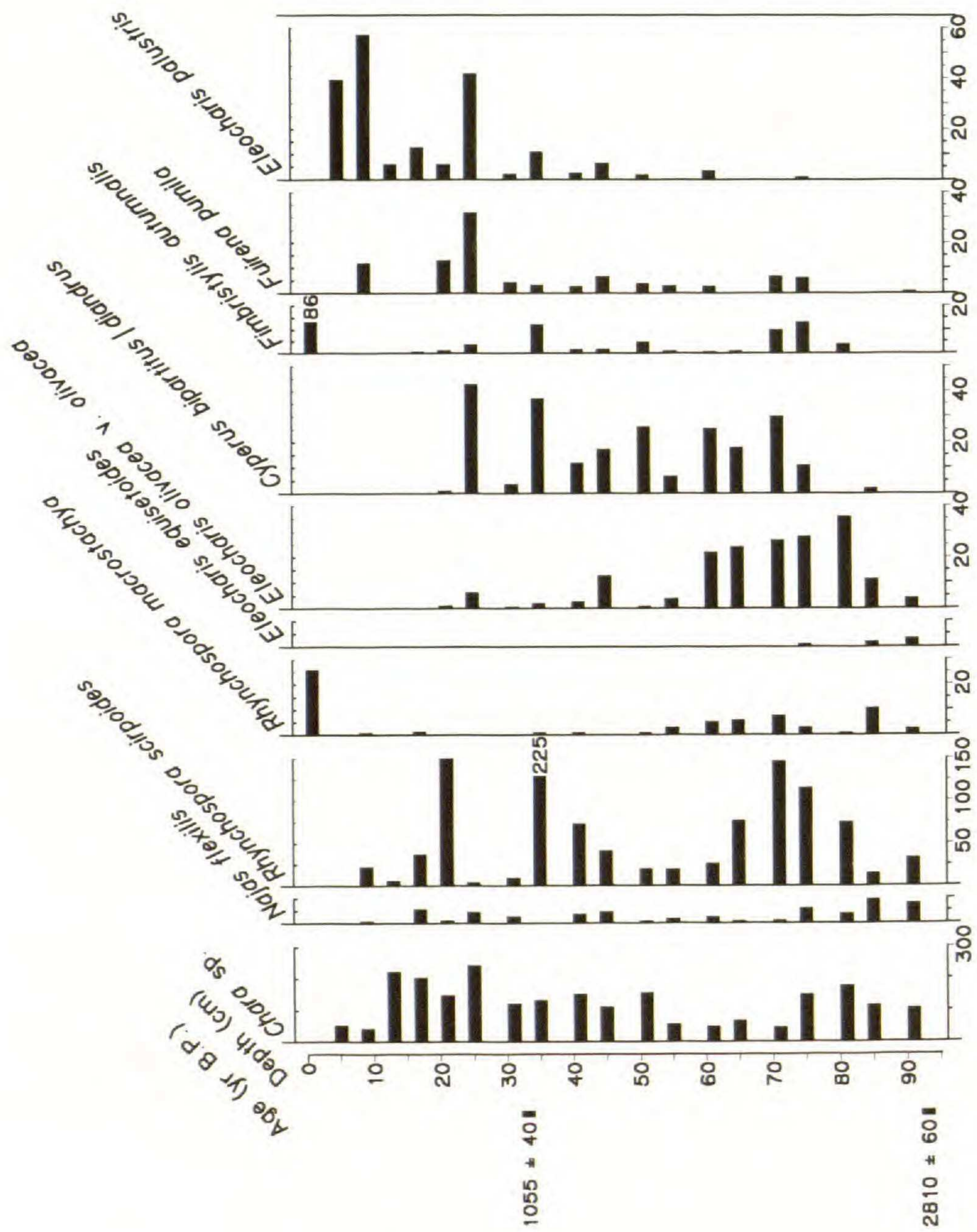
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Figure 2. Pollen percentage diagram from Portage Marsh Core 1. Only selected taxa are included. Modified from Singer et al. (1996).

Figure 3. Plant macrofossil concentration diagram from Portage Marsh Core 1. Only selected taxa are included. Modified from Singer et al. (1996).









The four Coastal Plain species (*Rhynchospora scirpoides*, *R. macrostachya*, *Fuirena pumila*, and *Eleocharis equisetoides*) colonized the marsh between 5700 and 4500 yr B.P. (Figure 3). Of these, *E. equisetoides* is a shallow-water submersed plant, while *R. scirpoides*, *R. macrostachya*, and *F. pumila* are emergents of mudflats and other exposed, wet sites. *Rhynchospora scirpoides* and *F. pumila* are annuals.

*Quercus* savanna persisted on uplands of northwestern Indiana until Euro-American land clearance (Bacone et al. 1980), although mesic forests of *Acer*, *Betula*, and *Fagus* developed locally on sites with fine-textured soils during the late Holocene (ca. 3000 yr B.P.; Singer et al. 1996; Futyma 1985; Bailey 1972). The mixed assemblage of emergent, submersed, and floating-leaved plants persisted in Portage Marsh until Euro-American disturbance, although the emergent flora underwent some changes after 2800 yr B.P. (Figures 3 and 4). *Eleocharis equisetoides* disappeared ca. 2800 yr B.P., but *Rhynchospora scirpoides* and *Fuirena pumila* may have persisted in the marsh until Euro-American disturbance (Figures 3 and 4). The exact timing of their extirpation is uncertain, owing to a depositional hiatus spanning at least the 19th and early 20th centuries (Singer et al. 1996). *Rhynchospora macrostachya* populations evidently have persisted in the basin throughout the past 4500 years (Figures 3 and 4).

#### DISCUSSION

**Holocene climate change in the Great Lakes region.** The changes in regional vegetation, wetland vegetation, and water level observed in the Portage Marsh record show a consistent climatic pattern: (a) cool, moist late-glacial conditions (>10,000 yr B.P.); (b) warm, moist climate during the early Holocene (10,000 to 5700 yr B.P.); (c) rapid transition toward drier climate during the mid-Holocene (5700 to 2800 yr B.P.); and (d) a trend toward cooler, moister conditions in the late Holocene (2800 yr B.P. to

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Figure 4. Plant macrofossil concentration diagram from Portage Marsh Core 2. Core 2 includes only the top meter of sediments, spanning the past 2800 radiocarbon years. Only selected taxa are included. Modified from Singer et al. (1996).

present). This fits a regional climate pattern documented in eastern Iowa, northern Illinois, southern Wisconsin, northern Indiana, and southern Michigan (Webb et al. 1983; Baker et al. 1992, 1996; Singer et al. 1996).

The Holocene period of highest effective moisture (i.e., precipitation minus evapo-transpiration) in the southern Lake Michigan region, 10,000 to 6000 yr B.P., corresponds to the Milankovitch summer insolation maximum following withdrawal of the Laurentide ice sheet (Kutzbach and Webb 1991). Wright (1992) proposed that higher summer insolation amplified monsoonal flow into the southern Great Lakes region, increasing summer rainfall. Reduction in monsoonal flow as summer insolation decreased after 6000 yr B.P. led to drier conditions. Continuing late Holocene reduction in summer insolation led to cooling and increased effective moisture after 3000 yr B.P. (Wright 1992; T. Webb et al. 1993).

The eastern Great Lakes, St. Lawrence valley, and Hudson–Mohawk lowlands experienced a different sequence of Holocene climatic changes. These regions also were cool and moist during the late-glacial period (>10,000 yr B.P.). However, they were warmest and driest during the early Holocene (9000 to 6000 yr B.P.; Gaudreau and Webb 1986; Webb 1990; R. S. Webb et al. 1993; T. Webb et al. 1993). High summer temperatures were related to the summer insolation maximum. Regional lake levels were low (Webb 1990), and upland vegetation was relatively xeric (R. S. Webb et al. 1993). Summer precipitation may have been low because summer storm tracks were shifted north (relative to today) along the steep thermal gradient at the edge of the Laurentide ice sheet (Webb 1990), which occupied much of eastern Canada from 9000 to 7000 yr B.P. (Dyke and Prest 1987). Effective moisture increased after 7000 yr B.P. (R. S. Webb et al. 1993), and the region has undergone a cooling trend for the past 5000 years (Gaudreau and Webb 1986; T. Webb et al. 1993).

**Climate change and the origin of coastal plain disjunctions.** Hypotheses proposed to explain the Coastal Plain disjunctions in the Great Lakes region fall into two general categories: (1) Holocene long-distance dispersal from the Coastal Plain populations, and (2) late-glacial migration along the ancestral Great Lakes and their outlets in the St. Lawrence and Hudson–Mohawk valleys and up the Mississippi and Illinois River

valleys (Peattie 1922; Keddy 1981; Reznicek 1994). Long-distance dispersal is unlikely in view of the number of species and the magnitude of distances (800–1000 km from the Atlantic Coastal Plain to the central Great Lakes), although it cannot be ruled out with certainty. Plant dispersal events on the order of  $10^2$  km have been recorded during the Holocene, but plant dispersal over distances of  $10^3$  km appears to be very rare (Clark et al. 1998).

Peattie (1922) and others have proposed that the Coastal Plain plants migrated inland along a continuous corridor of suitable habitat that existed during the late-glacial. Reznicek (1994) cites geological evidence that such a continuous corridor never existed, but notes that suitable local habitats may have existed intermittently along the migration routes. Thus, the migration would have consisted of site-to-site dispersal events on the order of  $10^1$ – $10^2$  km. Peattie's original migration hypothesis and its derivatives assume that the migration took place during the late-glacial, and that the disjuncts have occupied their modern ranges during all or most of the Holocene. Local populations persisting along the migration route presumably were extirpated during the Holocene.

The paleoecological record of four of these disjunct species at Portage Marsh, together with a consideration of the postglacial climatic and biogeographic history of eastern North America, suggests an alternative mechanism for the disjunction. These species colonized Portage Marsh between 5700 and 4500 yr B.P., when regional climate change led to the establishment of a marsh with a fluctuating water level. Under the hypotheses of late-glacial migration, mid-Holocene establishment at Portage Marsh would have represented addition of another population to many already existing in the southern Lake Michigan region at the time. However, populations at other wetlands in the region may also have been established after 5700 yr B.P. Most of the wetlands where these species have been observed (Peattie 1930; Wilhelm 1990; Wilcox 1995) were formed during or after construction of the early Toleston Beach complex 4000–5000 yr B.P. (Chrzas-towski and Thompson 1992; Thompson 1992). Inland basins that already existed during the early Holocene would, like Portage Marsh, have undergone water level declines 5700 yr B.P. Thus, establishment of most and perhaps all disjunct populations near southern Lake Michigan occurred during the mid- and late Holocene, as suitable habitats were formed by climate-induced shal-

lowing of existing basins and by creation of shallow wetlands by coastal processes.

These species may have colonized the southern Lake Michigan region from the eastern Great Lakes region during the mid-Holocene. Isolated populations of some of these species occur near Lakes Erie and Ontario (Reznicek 1994). Those populations may be remnants of more extensive early Holocene populations. Shallow wetland habitats on suitable substrates may have been more extensive in the eastern Great Lakes region during the relatively dry early Holocene. Such habitats would have disappeared during the mid- to late Holocene owing to increasing effective moisture (T. Webb et al. 1993) and to drowning of coastal wetlands by rising lake levels in the Erie and Ontario basins (Anderson and Lewis 1985; Coakley and Lewis 1985; Coakley and Karrow 1994).

Thus, these disjunct species may have undergone geographic range shifts in response to geographic movements in their "habitat space" (e.g., Huntley and Webb 1989). That "habitat space" is directly linked to regional climate: regional climate constrains local hydrology via precipitation and evapo-transpiration, and the local hydrology constrains the local habitat features experienced directly by the plants (e.g., average and extreme water levels, frequency and magnitude of inundation and drawdown). We hypothesize that populations were established in the eastern Great Lakes region during the early Holocene on shallow wetlands, which were perhaps widespread owing to dry climate and low lake levels. Most of those populations were extirpated in the mid- and late Holocene as effective moisture increased and lake levels rose. To the west, however, increasingly dry conditions and coastal processes created suitable habitats along southern Lake Michigan during the mid- to late Holocene. Dispersal events on the order of  $10^2$  km led to establishment of populations in these new habitats, which persisted until Euro-American settlement. This hypothesis, like others proposed to explain the disjunction, is speculative. However, it could be tested against alternatives by paleoecological studies of other wetlands in the southern Lake Michigan and eastern Great Lakes regions.

An alternative migration route, proposed by Peattie (1922) and further discussed by Reznicek (1994), is from the Gulf Coastal Plain to the central Great Lakes via the Mississippi and Illinois River valleys. Disjunct populations of several Coastal Plain spe-

cies occur in the upper Mississippi and Illinois valleys, although none of the four species documented at Portage Marsh are among them. It is possible that the disjunct Coastal Plain flora of the central Great Lakes region consists of a mixture of species that moved westward from the eastern Great Lakes and northward from the Mississippi valley (Reznicek 1994). Unfortunately, Holocene vegetational and climatic changes in the lower and central Mississippi valley and adjacent uplands are poorly documented (T. Webb et al. 1993; Jackson et al. 1997).

**Quaternary biogeography and disjunct populations.** Late Quaternary pollen and macrofossil records indicate that the post-glacial climatic and vegetational history of eastern North America was dynamic and spatially complex. Regional and subcontinental mapping of pollen and macrofossil data indicates spatial shifts in range boundaries and population centers of upland tree and shrub species throughout the Holocene (Gaudreau 1988; Webb 1988; Jackson et al. 1997). These movements were not simply unidirectional migrations from glacial “refugia” in response to post-glacial warming. Rather, they consisted of complex and continual adjustments to climatic changes that occurred throughout the Holocene (Webb 1988; Huntley and Webb 1989). Species ranges moved in different directions at different times, and range-boundary expansions of some species were followed by contractions. Studies at finer scales indicate that ranges of tree species shifted along local elevational and edaphic gradients in response to Holocene climatic changes (Brubaker 1975; Jackson 1989; Spear et al. 1994).

Historical explanations of range disjunctions traditionally have emphasized single disjunction-forming events followed by relative stasis. For example, “relict” disjuncts, local vestiges of past regional climate, typically are assumed to have remained *in situ* in locally suitable habitats since the climatic change that led to disappearance of regional populations. Other disjunctions are viewed as remnants of formerly continuous populations that were separated by a unique geological event (e.g., inundation of land bridges, drying of proglacial lakes and outlets). While some disjunct remnants of past climates or events may have persisted in their present locations for thousands of years, direct paleoecological confirmations of such long-term persistence are few. Many disjunct populations probably have complex and dynamic histo-

ries, consisting of isolation (via either jump-dispersal or range contraction of the core population) followed by geographic shifts in both the core population and the disjunct populations in response to environmental change. Paleoecological studies are essential to document such shifts and test disjunction hypotheses.

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